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BIOLOGY AND IMMATURE STAGES OF *DRYOMYZA ANILIS* FALLÉN (DIPTERA: DRYOMYZIDAE)[1]

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Abstract.—Information is presented on the life cycle of *Dryomyza anilis* Fallén, the saprophagous larvae of which feed on decaying animal matter and decaying fungi. Data on the habitat, behavior, feeding habits, and phenology of adults and immature stages are presented. The egg, three larval instars, and puparium are described in detail. The taxonomy of the species, and the systematics of the Dryomyzidae, are discussed briefly.

Information on the biology and immature stages of the Dryomyzidae is fragmentary and scattered in the literature. Burger et al. (1980) described the second- and third-instar larva and the life history of *Oedoparena glauca* (Coquillett), a predator of barnacles on the west coast of North America. Steyskal (1957) illustrated an egg of *Dryomyza flaveola* (Fabricius) that was dissected from an adult, and Hinton (1960, 1981) described and illustrated eggs of the same species, stating that they were usually laid on the vertical sides of cow pats in shaded areas of fields or woods. Burger et al. (1980) presented previously unpublished rearing records for *D. simplex* Loew, prepared by B. A. Foote, which indicate that this species, as well as *D. anilis* Fallén, can develop from egg to pupa on dead animal matter, but not on decaying plant matter.

The literature dealing with the biology of *D. anilis* was reviewed by Smith (1980). This species has been found in association with rotting fungi, carrion, and excrement. Portschinsky (1910) illustrated the egg and the terminal segment of the larva, and Smith (1980) illustrated and briefly described the mature larva. Foote (in Burger et al., 1980) found that larvae of *D. anilis* fed and pupated on hamburger, dead earthworms, dead crane flies, dead polygyrid snails, a dead milkweed caterpillar, a dead slug, and rotting agaric mushrooms. Larvae did not attain maturity when given rotting grass, decaying pumpkin flesh, decaying lettuce, or cow manure.

The Dryomyzidae were usually considered a part of the Sciomyzidae by earlier authors, but they are now considered a separate family with two subfamilies, the Dryomyzinae and Helcomyzinae (Griffiths, 1972; Mathis and Steyskal, 1980), or, as in this paper, they are considered two separate families, the Dryomyzidae and Helcomyzidae (Barnes, 1981). The Dryomyzidae can be separated from the Helcomyzidae by the closely spaced first antennal segments, protruding oral margin,

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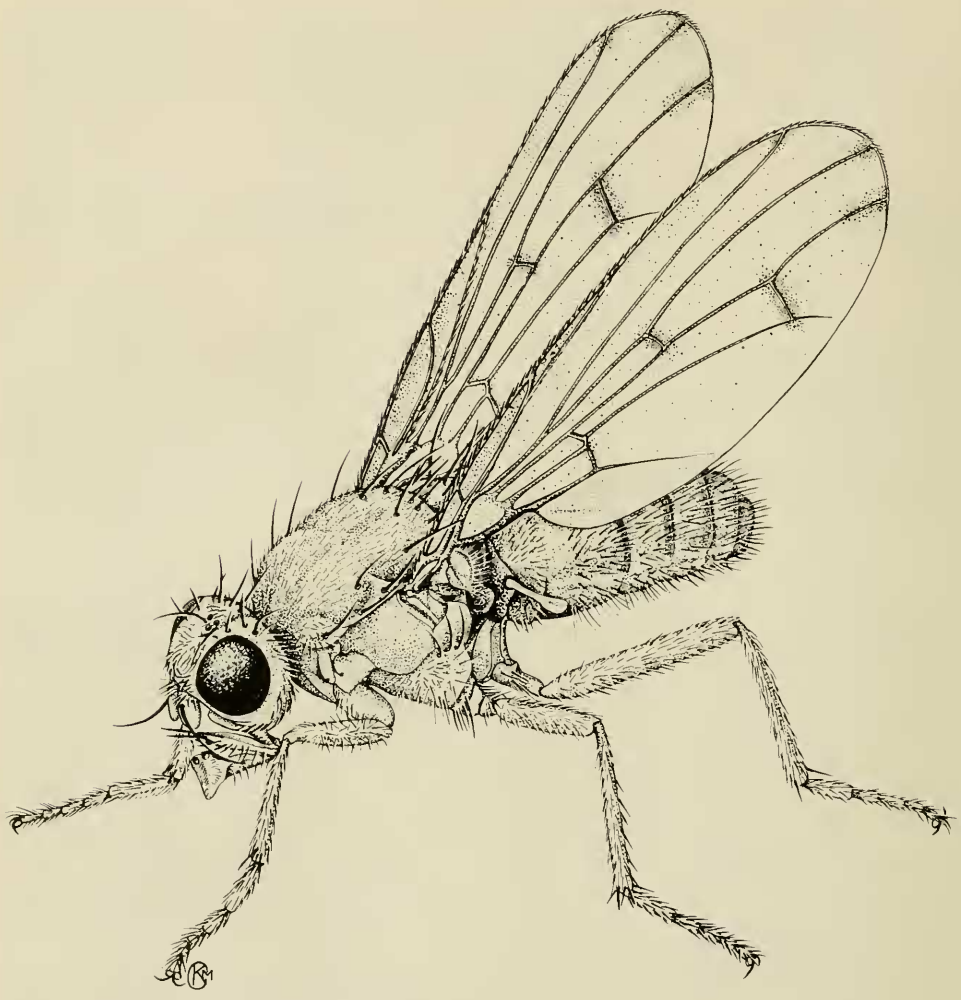


Fig. 1. *Dryomyza anilis*, adult female.

strap-shaped or oval prosternum that is not joined to the propleura, and lack of costal spines. Two genera, *Dryomyza*, with ten species, and *Oedoparena*, with two species, are presently recognized in the Dryomyzidae (Steyskal, 1957, 1958, 1962; Mathis and Steyskal, 1980).

Dryomyza anilis is widely distributed in the Palaearctic and Nearctic Regions. Adults (Fig. 1) are light brown and medium sized, ranging in overall length from about 7 to about 14 mm. It can be separated from other species of Dryomyzidae by the nearly bare arista, covered lunule, and well developed prostigmatic and prescutellar bristles.

Rearing Methods

Laboratory rearings were kept in an incubator at 20°C under a LD 16:8 lighting schedule, unless otherwise indicated. Adults were held in clear plastic vials (5.0 × 8.5 cm) fitted with screen caps. A layer of cotton on the bottom of each vial

moistened with a 0.1% aqueous solution of the mold inhibitor Lexgard M®[2] helped to maintain high humidity. A wooden applicator stick provided a resting site for the flies. Adults fed readily on an artificial diet consisting of honey, brewer's yeast, and dehydrated milk.

Eggs were allowed to hatch in the vials in which they were laid, and potential food items were placed on the cotton substrate. Larvae were transferred to fresh rearing vials when the old ones became overgrown with mold. Several larvae were reared together in each vial, so it was not possible to determine the duration of each stadium for individual larvae, but it was possible to determine the number of days after eclosion that molts and pupariation occurred for each group of larvae by observing when cast exuviae and puparia appeared in the vials. Puparia were placed in individual glass vials containing a layer of moist cotton. The vials were plugged with dry cotton and placed in incubators to await emergence of adults.

Biology

Dryomyza anilis is a common species in Europe and northern North America. The specimens used in this study were collected at Black Creek Swamp, on Koontz Rd., Voorheesville, New York (42°39′57″N, 73°58′05″W). They were collected by sweeping *Aster simplex* Willdenow and *Onoclea sensibilis* Linnaeus, the dominant low vegetation under the thin canopy of *Ulmus rubra* Muhlenberg and *Fraxinus pennsylvanica* Marshall. The locality was frequently flooded after a heavy rain, and it is surrounded by a *Typha* and *Sparganium* marsh.

Laboratory-reared males lived 28–178 days (mean ± SD, 83.0 ± 50.4; n = 13), and females lived 26–167 days (79.2 ± 38.9; n = 20). Field-collected and laboratory-reared adults mated frequently in the laboratory. No courtship behavior was observed. A male mounts a female and, facing in the same direction, persuades her to spread her wings with the assistance of the tip of his abdomen and his hind tarsi. The male's fore tarsi are placed either on the substrate or the female's head, his mid tarsi are placed either on the substrate or the bases of the female's wings, and his hind tarsi usually grasp the female's abdomen near the midlateral line of segment 3 or 4. The male's wings remain in the rest position over the abdomen during mating.

During this investigation eggs were not found in the field, but Portschinsky (1910) found them on the surface of human excrement, and the excrement was often entirely covered by eggs. The eggs were laid singly, and they acquired the coloration of the substrate. In the laboratory, eggs were laid on a variety of materials that were introduced into the breeding vials, including dead insects, chicken liver, hamburger, and the moist cotton substrate. Eggs are rarely deposited on a dry surface. If the surface on which they are laid is liquid, the eggs sink into the material part way, but the upper surface of the eggs and the lateral flanges (Fig. 2) remain exposed to the air. If an egg is forced below the surface of the liquid the lateral flanges fold upward, and a bubble of air is held in contact with the upper surface of the flanges and the dorsal surface of the egg. The lower surface of the egg, including the underside of the flanges, is shiny and sticky. Eggs are

[2] Inolex Corporation, Philadelphia, Pennsylvania.

usually scattered over a surface one by one, but sometimes they are deposited side by side in rows of 2–5.

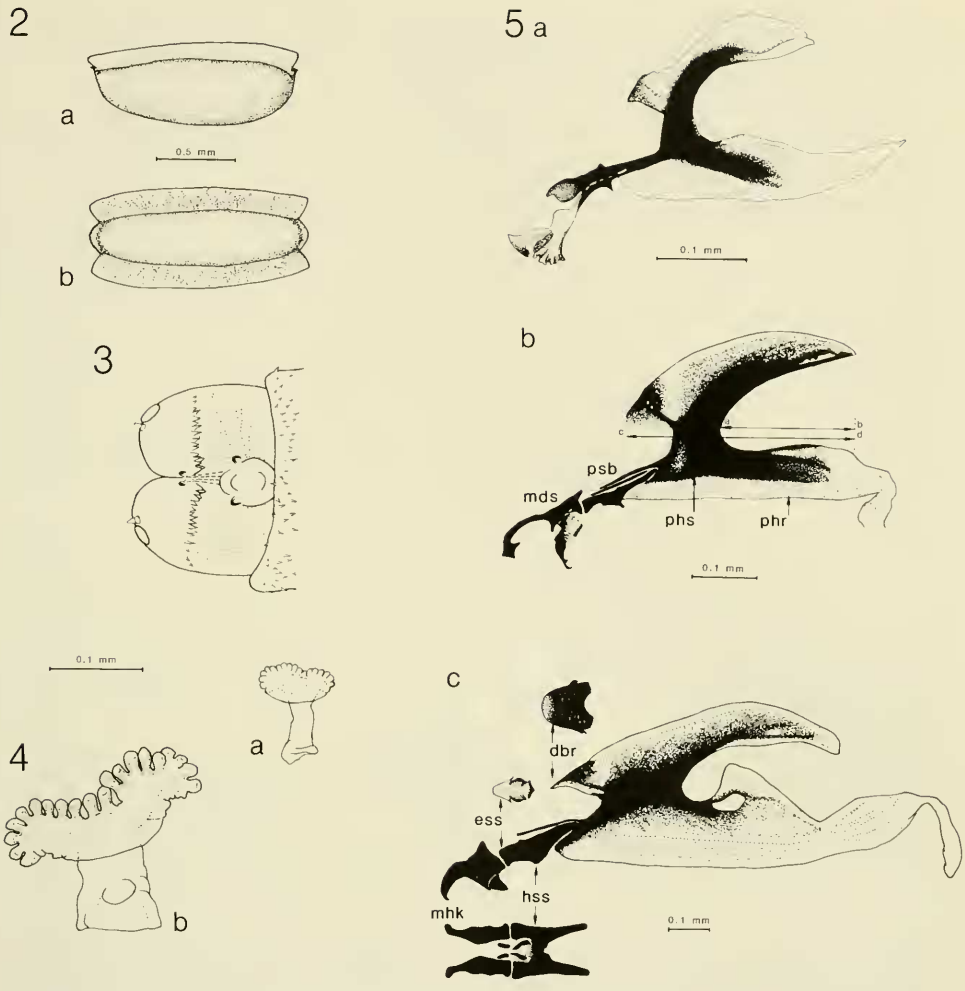
Eggs were laid by field-collected females within a few days after they were taken into the laboratory, regardless of when they were collected. Females were collected between May 26 and September 25, 1981, and all of them produced fertile eggs. They usually oviposited every 2–10 days, depositing as many as 48 eggs in a single day, and as many as 208 eggs altogether. Laboratory-reared females began to lay eggs 30–81 days (49.5 ± 19.8; $n = 11$) after they emerged from puparia. The egg incubation period is short; 29 eggs that were laid between 1:00 and 4:00 PM one day hatched between 3:47 and 4:14 PM the next day, so the minimum incubation period was 23 h 47 m, and the maximum was 27 h 14 m.

At eclosion, the chorion at the anterior end of the egg splits, and the larva escapes. The young larvae search for a soft spot or crevice into which they burrow, leaving only the posterior spiracles exposed. In laboratory rearings the larvae frequently congregated in the moist cotton beneath their food source, and cast exuviae were often found in this area following molting.

Larvae fed readily on a variety of dead, and often putrid, animal matter. Successful laboratory rearings were accomplished using dead, crushed insects, such as June beetles (*Phyllophaga* sp.), carrion beetles (*Nicrophorus* sp.), dytiscid beetles, dobsonflies (*Corydalus cornutus* (Linnaeus)), and calliphorid flies, and rotting chicken liver and hamburger as food sources. In one rearing, 41 newly hatched first-instar larvae were given both chicken liver and June beetles. Some of the larvae fed and molted to the second instar on the chicken liver, but within two days after starting the rearing all larvae were found to be feeding on the June beetles in preference to the liver. Larvae did not feed on dead, crushed gypsy moth larvae or pupae (*Lymantria dispar* (Linnaeus)), nor on a rotting polypore fungus (*Polyporus squamosus* Micheli: Fries). Six larvae that were given only decaying lettuce died within two days, but not before one of them molted to the second instar. One of 33 larvae that were given only decaying spinach formed a puparium seven days after hatching, but the puparium was small (only 4 mm long), and it did not yield an adult fly.

The first molt of the fly larvae occurred within one day after eclosion, the second molt occurred within two days after eclosion, and the larvae formed puparia 6–8 days (7.1 ± 0.7; $n = 39$) after eclosion. Larvae usually burrowed deep into the moist cotton in the rearing vials before forming puparia, but they also frequently pupariated on the surface of the cotton under the food source. Adults emerged 18–27 days (20.4 ± 1.6; $n = 46$) after pupariation. Reared females produced fertile eggs and apparently healthy larvae.

Evidence concerning overwintering stages and diapause in *Dryomyza anilis* is inconclusive. Adults were not found in the field until May 26, but a gravid female was collected as late as September 25. She produced 152 fertile eggs by October 13, then stopped ovipositing, but lived until January 29. Puparia were reared from her eggs at 20°C and LD 16:8, and within 1–7 days after preparation, in early to mid October, they were placed in an incubator that simulated mild winter conditions. The daily temperature range of 10–21°C and the lighting schedule of LD 12.5:11.5 in October were gradually changed to 3–10°C and LD 9:15 in January, where they remained until March, when the trends were reversed. On two occasions, once in late February and once in early April, the incubator malfunctioned, and the temperature dropped to −1.5°C for a short period. From a



Figs. 2–5. *Dryomyza anilis*. 2, Egg, lateral (a) and dorsal (b) views. 3, Segment 1, 1st-instar larva, ventral view. 4, Anterior spiracles of 2nd- (a) and 3rd- (b) instar larvae. 5, Cephalopharyngeal skeletons of 1st- (a), 2nd- (b), and 3rd- (c) instar larvae (shown separately: ess and dbr in dorsal view, mds and hss in ventral view). Indentation index = ab/cd ×100. Abbreviations: dbr, dorsal bridge; ess, epistomal sclerite; hss, hypostomal sclerite; mds, mandibular sclerite; mhk, mouth-hook; phr, pharyngeal ridges; phs, pharyngeal sclerite; psb, parastomal bar.

total of 70 puparia, 31 adults emerged in the incubator from November 5 to January 25. The remaining puparia were warmed to 20°C, and the lighting schedule was adjusted to LD 16:8, on May 5. Adults emerged from seven more puparia between May 20 and June 11. No adults emerged from the remaining 32 puparia, all of which eventually turned moldy.

Descriptions of Immature Stages

Egg (Fig. 2).—Length 1.22–1.37 mm, greatest width 0.41–0.48 mm. Creamy white, elongate, somewhat tapered anteriorly. Paired, elongate, ribbon-like flanges present dorsolaterally; each flange with anterior end rounded, posterior end more

acute; dorsal surface covered with fine, radiating ridges. Small curved flanges present anteriorly and posteriorly. Surface of egg, excluding lateral flanges, wholly covered with fine, honeycomb-like reticulation.

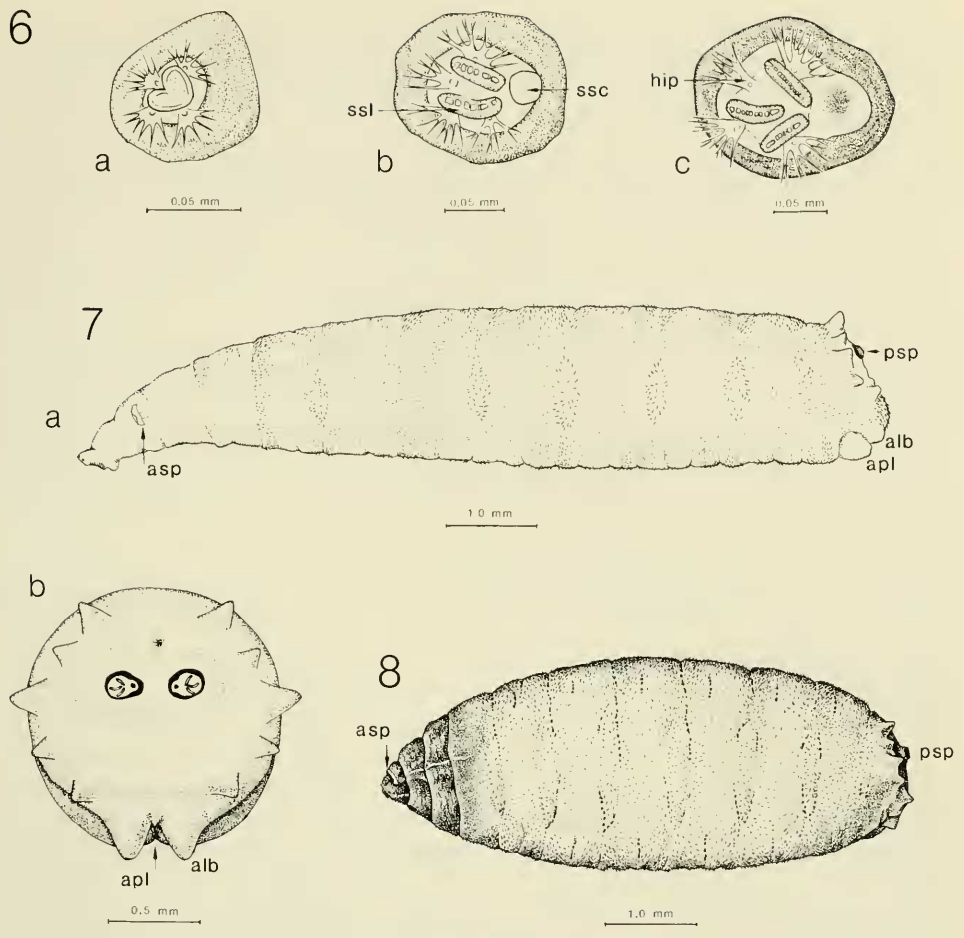
Larva (Figs. 3–7).—*First instar:* Length 1.67–2.96 mm, greatest width 0.41–0.59 mm. Anterior spiracles absent. Posterior spiracular plates (Fig. 6a) pale yellow, each with a B-shaped spiracular opening and 4 sets of peripheral, palmately-branched hair-like processes about ½ as long as diameter of plate.

Cephalopharyngeal skeleton (Fig. 5a) brown to black, 0.28–0.33 mm long; indentation index 67–77. Segment 1 with rows of 3–4 darkly pigmented and 13–14 smaller, colorless spinules extending laterally from each side of midline ventrally (Fig. 3). Paired, lightly pigmented, irregular sclerites, apparently associated with oral grooves, present below rows of spinules. Lateral bars fused anteriorly, forming a small, mouth-hook-like structure; each bar fused posteriorly to anteroventral edge of respective pharyngeal sclerite. Paired, narrow, elongate, weakly fused sclerites present below anterior ends of lateral bars. Pharyngeal sclerites without windows; lightly pigmented bridge present anterodorsally, pharyngeal ridges present between ventral cornua.

Second instar: Similar to 3rd-instar larva. Length 2.74–4.71 mm, greatest width 0.61–0.91 mm. Anterior spiracles (Fig. 4a) pale yellow; reniform apical part bearing 19–20 rudimentary papillae. Posterior spiracular plates (Fig. 6b) pale yellowish brown, each with 2 elongate spiracular slits, a white spiracular scar, and 4 sets of peripheral, palmately branched, hair-like processes about ⅓ as long as diameter of plate; ventral spiracular slit upcurved at both ends.

Cephalopharyngeal skeleton (Fig. 5b) brown to black, 0.57–0.61 mm long; indentation index 60–67. Mandibular sclerites long, narrow; mouth-hooks triangular in lateral view, bearing 3–4 ventral teeth in anteroventral view, connected to mandibular sclerites by long, narrow, curved bars. Dentary sclerites long, narrow, irregularly shaped, pointed ventrally, lightly pigmented posterodorsally. Small, paired, quadrate sclerites present between mandibular sclerites in area of dentary sclerites. Hypostomal sclerite with posterior end free from pharyngeal sclerites. Pharyngeal sclerites with long, narrow windows posteroventrally on dorsal cornua and posterodorsally on ventral cornua; bridge present anterodorsally. Pharyngeal ridges present between ventral cornua.

Third instar (Fig. 7): Length 4.10–9.42 mm; greatest width 0.76–2.13 mm. White; integument translucent. Body elongate, conicocylindrical; anterior end strongly tapered; posterior ⅔ relatively uniform in width; posterior end truncate, strongly sloping. Primary and secondary integumentary folds weak. Tubercles absent from segments 1–11. Segment 1 strongly bilobed apically, each lobe with a short, pale yellowish brown, 2-segmented sensory papilla dorso-apically and a pair of circular sensory plates ventro-apically; oral grooves present. Posterior portion covered with fine, unicuspid, posteriorly-directed spinules. Segment 2 bearing paired, yellowish to yellowish brown, reniform, transverse anterior spiracles posterolaterally (Fig. 4b); spiracles projecting nearly perpendicular to body, each bearing 19–24 papillae. Segments 2–3 with fine, unicuspid, colorless spinules, particularly dense dorsally and anteriorly. Segments 4–11 covered with larger, unicuspid, yellowish brown spinules dorsally and laterally; with spinules denser and stouter at anterior end of each segment ventrally. Segments 5–11 with poorly developed fusiform welts posterolaterally. Segment 12 covered with spinules dorsally, laterally, and ventrally; bearing anal plate, paired anal lobes, minute ven-



Figs. 6–8. *Dryomyza anilis*. 6, Posterior spiracular plates of 1st- (a), 2nd- (b), and 3rd- (c) instar larvae. 7, 3rd-instar larva, lateral (a) and posterodorsal (b) views. 8, Puparium, lateral view. Abbreviations: alb, anal lobe; apl, anal plate; asp, anterior spiracle; hip, hair-like interspiracular process; psp, posterior spiracle; ssc, spiracular scar; ssl, spiracular slit.

tromedial lobe, and spiracular disc posteriorly. Anal plate white to yellowish brown, strongly wrinkled, transverse, ovoid, lacking spinules; anus invaginated. Anal lobes posterior to anal plate short, stout, covered with spinules. Posterior spiracular disc (Fig. 7b) with spinules peripherally and ventromedially, with 5 pairs of spinule-covered, conical, peripheral lobes and 2 dorsocentral spiracular plates. Dorsal, dorsolateral, lateral, ventrolateral, and ventral lobes about 1.2, 0.6, 1.5, 0.8, and 1.0 times as long as diameter of spiracular plates, respectively. Spiracular plates (Fig. 6c) subcircular, yellowish brown to brown, each with 3 elongate-oval, diverging spiracular slits at 40–45° angle to each other, 1 circular, brown spiracular scar, and 4 colorless, palmately branched, hair-like interspiracular processes about ⅓ as long as diameter of spiracular plates; middle spiracular slit curved upwards at both ends.

Cephalopharyngeal skeleton (Fig. 5c) dark brown to black, 0.93–1.05 mm long; indentation index 50–56. Mandibular sclerites well developed, paired, separate,

without accessory teeth below curved mouth-hooks, with 1 small window centrally. Dentary sclerites paired, separate, near posteroventral margin of mandibular sclerites. Epistomal sclerite small, lightly pigmented not fused with parastomal bars, located between anterior rami of hypostomal sclerite, loosely articulated with paired, narrow, strap-like sclerites that nearly reach posterior end of hypostomal sclerite. Parastomal bars narrow, darkly pigmented; posterior ends fused to pharyngeal sclerites. Hypostomal sclerite H-shaped, not fused posteriorly to pharyngeal sclerites; anterior rami about ½ length of posterior rami and wider than posterior rami; hypostomal bridge notched posteriorly. Small, paired sclerites present between anterior rami of hypostomal sclerite and between dentary sclerites. Pharyngeal sclerites with anterodorsal bridge joining anterior ends of dorsal cornua, and with anteroventral projections lying below posterior rami of hypostomal sclerite; anterodorsal bridge lightly pigmented anteriorly, emarginate posteriorly, with several small windows on each side of midline; dorsal cornua narrower than ventral cornua, with elongate window posteroventrally; ventral cornua lightly pigmented posteroventrally and on mid-dorsal lobe, with large window on mid-dorsal lobe. Pharyngeal ridges between ventral cornua well developed.

Puparium (Fig. 8).—Length 4.41–6.23 mm, greatest width 1.75–2.51 mm. Light yellowish brown to reddish brown; segments 2–4 and 12 often darker than remainder. Primary and secondary integumentary folds indistinct. Integument densely wrinkled on segments 2–4 and 12. Puparium elongate, subcylindrical; dorsal surface more convex than ventral surface. Segment 1 invaginated. Segments 2–4 strongly tapered, somewhat flattened dorsoventrally. Anterior spiracles dark reddish brown, sessile, transverse, on anterolateral angles of dorsal cephalic cap, projecting anterolaterally. Spinules arranged as in 3rd-instar larva. Punctiform papilla vestiges distinct, darkly pigmented, arranged in a consistent pattern on segments 5–11—a transverse row posterodorsally, in rows on dorsal and ventral margins of posterolateral fusiform welts, in 2 short, paired rows dorsolaterally and 1 short row mid-dorsally, and in 3 irregular, transverse rows ventrally. Segment 12 truncate, indented mid-dorsally; lobes as in 3rd-instar larva, but usually somewhat reduced. Posterior spiracular plates dark yellowish brown to reddish brown; spiracular slits yellowish brown; spiracular scar dark brown to black. Anal plate dark reddish brown, somewhat invaginated. Cephalopharyngeal skeleton as in 3rd-instar larva, appressed to ventral cephalic cap.

Discussion

Adults of *Dryomyza anilis* have been found in association with human excrement (Portschinsky, 1910; Skidmore, 1978), fox and pheasant carrion (Smith, 1975, 1980), and malodorous stinkhorn fungi (Parmenter, 1951; Smith, 1956). Eggs have been found on human excrement (Portschinsky, 1910), and larvae have been found in pheasant carrion (Smith, 1980). The laboratory rearings described in this paper and in Burger et al. (1980) show that *D. anilis* can be successfully reared on a variety of dead annelids, molluscs, insects, vertebrates, and rotting fungi. The presence of well developed pharyngeal ridges in all three larval stages indicates that the larvae are probably deriving most of their nutrition from particulate material, including micro-organisms that colonize rotting organic material. Pharyngeal ridges are commonly found in saprophagous cyclorrhaphous lar-

vae, and they have been found to effectively separate bacteria and other microorganisms from liquid entering the pharynx, thus preventing the uptake of excess, non-nutritious liquid. Larvae that feed on living tissue lack such ridges (Dowding, 1967, 1968).

The cephalopharyngeal skeleton of the mature larva fits the characterization of the generalized type found in saprophagous cyclorrhaphous Diptera, as given by Miller and Foote (1976). The mandibular sclerites, hypostomal sclerite, and pharyngeal sclerites are not fused to each other. Paired dentary sclerites are present. The narrow parastomal bars are fused to the pharyngeal sclerites, but not to the epistomal sclerite. An anterodorsal bridge joins the pharyngeal sclerites. The hypostomal sclerite is H-shaped. Among the Sciomyzoidea this type of cephalopharyngeal skeleton is also characteristic of the Helosciomyzidae (Steyskal and Knutson, 1978; Barnes, 1980a, b). *D. anilis* lacks the apomorphic ventral arch characteristic of the Sciomyzidae (Knutson et al., 1970; Griffiths, 1972). Comparisons cannot be made with other families of Sciomyzoidea because there are too few thorough descriptions of larvae.

The egg of *D. anilis* seems particularly well adapted to survival on the type of substrate upon which it is laid. Like the eggs of some Anthomyiidae and Muscidae, it bears two dorsolateral flanges. These flanges appear to aid the egg in floating on the surface of a liquid or semiliquid substrate. The chorion quickly takes on the coloration of the substrate, thus affording the egg some camouflage. The short incubation period (about 24 h) reported here and by Portschinsky (1910) might give the species a competitive advantage in exploiting a limited resource, and it might also help prevent parasitism or predation of this vulnerable stage.

In this study, no predators or parasites of *D. anilis* were found, but Portschinsky (1910) reported that several larvae of *Mydaea urbana* (Meigen) (Diptera: Muscidae) destroyed a large population of *D. anilis* larvae on human excrement.

Diagnostic descriptions of larvae exist for less than five percent of the Nearctic species of cyclorrhaphous Diptera (Tesky, 1981). Good descriptions of the mature larvae of Helcomyzidae and Dryomyzidae now exist for only three species worldwide. Comparison of these descriptions reveals that mature larvae of the three species differ significantly in many respects. Larvae of *Helcomyza ustulata* Curtis (Helcomyzidae) have short posterior spiracular tubes and a strong, upwardly directed hook on each posterior spiracular plate, and lack well developed tubercles (Egglishaw, 1960). Those of *Oedoparena glauca* (Dryomyzidae) have elongate posterior spiracular tubes, lack hooks on the posterior spiracular plates, and have well developed tubercles on segments 5–12 (Burger et al., 1980). Those of *D. anilis* have short posterior spiracular tubes, lack hooks on the posterior spiracular plates, and have well developed tubercles on segment 12 only. As larvae of more species of Dryomyzidae, Helcomyzidae, and other species of Cyclorrhapha are described these characters may not prove to be diagnostic, especially at the species level.

Based on adult morphology, the Dryomyzidae, Helcomyzidae, and Helosciomyzidae appear to be more closely related to each other than they are to other Sciomyzoidea (Barnes, 1981). At this time little can be said about these relationships, based on larval morphology. Too few species have been reared, and insufficient information is available on the immature stages.

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